# Home Range and Substrate Use by Two Family Groups of Red-cockaded Woodpeckers in the North Carolina Sandhills

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ABSTRACT.— Home range and foraging habitat use by two family groups of red-cockaded woodpeckers (*Picoides borealis*) were studied over the course of a year. Average year-round convex polygon home range size was 159 ha. One family group selected foraging areas of relatively high pine density within the home range, whereas the second exhibited no selection. Most foraging occurred on living pines as has been reported elsewhere. Overlap between the sexes in foraging niche, defined in terms of foraging substrates, was low during winter, when the percentage of activity spent feeding was greatest. These data suggest that food limitation, if it occurs at all, is most severe during early winter.

The red-cockaded woodpecker, Picoides borealis (Vieillot), a species endemic to the coastal plain of the southeastern United States (Murphey 1939, see Hooper et al. 1980 for a composite range map), is endangered because of the declining availability of suitable habitats (Jackson 1971, Thompson 1976, Lennartz et al. 1983). Its distribution is correlated with the distribution of longleaf pine forest types that are 60+ years old (Lennartz et al. 1983). Old living pines are known to be a critical resource for nest and roost cavities (Jackson et al. 1979). There has also been concern, because of the link with older forests, that those forests (age 60+ years) provide foraging conditions necessary for the survival of the species (Skorupa 1979, Ligon et al. 1986), but that has not been demonstrated. We undertook this study in the Sandhills of North Carolina, where the largest population of red-cockaded woodpeckers in North Carolina is located (Carter et al. 1983) and where very little is known of the foraging habits of this species. Our objectives were to describe foraging habits in the region, to test for selection of forest characteristics within home ranges that could be related to quality of foraging habitat, and to identify that time of year when resources are least abundant and hence habitat quality most critical.

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### **METHODS**

## STUDY AREA

The study was conducted on the Sandhills Game Land, Richmond Co., N.C. Uplands were predominantly longleaf pine (Pinus palustris)scrub oak (Quercus laevis, Q. marilandica, Q. incana, Q. margaretta)wiregrass (Aristida stricta) communities. Small stream margins and seepage slopes were characterized by pond pine (Pinus serotina) overstories and understories ranging from grass-sedge bog through swamp hardwoods. The gameland had been managed primarily for the production of timber and game. Longleaf pine had been harvested on a 100-year rotation and regenerated by seed tree cuts. Pond pine had been managed similarly but on an 80-year rotation. Prescribed burning had taken place on a 5-year rotation, except in northern bobwhite (Colinus virginianus) management areas, which had been burned on a 1- to 2year rotation. Areas under the long burning rotation had dense hardwood understories, whereas the more frequently burned areas had open, park-like understories. A general description of the vegetation of the Sandhills region has been presented by Wells and Shunk (1931).

## HOME RANGES

Two family groups of red-cockaded woodpeckers (group A and B) were randomly chosen from four family groups that were located within an area that was not to be logged during the study. All individuals in each group were color-banded. Once each month from August 1979 through July 1980, we followed one group for five continuous days of dawn-to-dusk tracking. Thus, each group was followed six times. When a group split while it was being tracked, we continued to follow the subgroup with the adult male. Locations taken at 5-minute intervals were recorded on an aerial photograph (1:12000). We also made zero-one scan samples (Altmann 1974) of behavior at 5-minute intervals, yielding an average of 747 observations per tracking period. Behaviors were categorized as foraging, resting, preening, and social conflict. We defined home ranges as the convex polygons enclosing all locations (Odum and Kuenzler 1955), and we estimated year-round home range for each group. Territories were defined by plotting territorial conflicts.

The resource base that we assumed to be available to each group was encompassed within its year-round home range. That assumption provided liberal estimates of resource availability, because convex polygons include areas of limited use and areas outside of territorial boundaries. Therefore, our assumption avoided the tautology of defining resource availability based on group locations and then testing for habitat selection with those same locations (Johnson 1980). Additionally, extraterritorial foraging may be important even if it occurs within the territories of other family groups, because the amount of time spent foraging within a territory and the time spent in territorial maintenance may depend upon territory quality (Ewald and Carpenter 1978).

A set of vegetation sampling points was selected from each overall home range by cluster sampling. Parallel transects traversing the home range were located perpendicular to an axis that was nearly parallel to most streams. Transects were located randomly along the axis but could not be less than 60 m apart. A sample point was located randomly within each 90-m segment of a transect. Distances were paced along a compass bearing. One hundred sample points were selected for group A, and 49 were selected for group B.

A random sample of foraging areas was selected from each tracking period. Foraging areas were defined as locations in the tracking itinerary in which the scan sample of behavior indicated that the family group was foraging. We randomly chose 25 foraging locations from each tracking period, except the final one for which 24 were chosen because of an error in a computer program. The samples averaged 5% of the foraging locations within tracking bouts. Each location was relocated in the field, and a random distance of up to 23 m (75 feet) was paced in a random compass direction to offset potential investigator bias in relocating points. As a further safeguard, distance and direction of each deviation were not ascertained until the point was relocated.

Each sampling point was the center of a Bitterlich variable-radius sampling plot (Husch et al. 1982) defined with a ten-factor prism. This method effectively samples trees of different sizes with plot sizes most suitable for them. For example, trees of 10 cm diameter at breast height (DBH) are sampled with a plot size of 33 m<sup>2</sup>, whereas trees of 45 cm DBH are sampled with a plot size of 691 m<sup>2</sup>. Species; DBH, rounded to the nearest 0.25 cm (= 0.1 inch); and tree height, rounded to the nearest 0.3 m (= 1 foot) were recorded for each tree. Pine stems less than 2.5 cm DBH were excluded from the analysis because the birds were not observed foraging on them. Hardwoods were considered understory trees if they were shorter than the mean pine height. Bole surface area was calculated as the surface area of a cone with base on the ground, apex at the tree height, and diameter (DBH) at breast height. For each plot, pine bole surface density (m<sup>2</sup>/ha) and tree density (trees/ha) were calculated (Husch et al. 1982). Means of bole surface per tree ( $m^2/tree$ ), pine DBH (cm), pine height (m), and understory hardwood height (m) were calculated as weighted means using the density expansion factor for each tree as its weight.

We used the Wilcoxon two-sample test (Sokal and Rohlf 1981) for all comparisons. Rank tests are recommended in resource-use studies because of the imprecision with which resource availability is measured (Johnson 1980). Additionally, data in this study were severely nonnormal. Calculations were performed with the Statistical Analysis System (SAS Institute 1982a, 1982b). Wilcoxon two-sample tests were performed with a user-written program, and home ranges were delineated and calculated with a procedure written by the senior author.

#### BEHAVIOR

Behavioral observations were made during the final 3 days of each tracking bout. Three 2-hour observation periods were conducted each day, beginning 1 hour after sunrise, 1 hour before the solar noon, and 3 hours before sunset. In May, when nestlings were being tended and tracking was difficult, observation periods were 3 hours long, and the beginning and ending times of the midday and evening periods were adjusted accordingly. During each observation period, a series of focal individuals was selected for sampling. When an observation bout was to begin, an individual was randomly selected from the birds available and followed for 5 minutes or until it flew from sight or became lost amidst the group. Instantaneous samples (Altmann 1974) of behavior and substrate were spoken into a cassette tape recorder at 15-second intervals that were timed with an electronic metronome.

Behaviors were lumped into functional categories. Categories included four types of foraging behavior, namely (1) gleaning, (2) peering and poking, (3) pecking, and (4) other, and non-foraging. Gleaning was picking food items from exposed bark surfaces as the bird moved forward or backward. Peering and poking consisted of peering into and poking the bill into bark crevices in search of prey. Side-to-side head movement was considerably greater than for gleaning. Movement along the substrate was slower, and stops were frequent. Pecking was subsurface foraging, including the pecking (percussion) and scaling categories of others (Jackson 1970, Ramey 1980, Hooper and Lennartz 1981). Pecking was perpendicular to the plane of bark when excavating for prey, or it was parallel to the bark plane to dislodge pieces. Scaling, the latter behavior, usually followed or preceeded pecking at a foraging spot. "Other" included obtaining seeds or fruits, drinking, and obtaining bone fragments. If a prey item was being handled at the time of sampling, the foraging technique used in capture was recorded as the current behavior. Post-capture handling of food for fledglings was classed as feeding of young instead of by the method of capture. The consequence of this was small because the process was a rare event and was seldom recorded. Non-foraging activities included all other behaviors.

Substrate classifications consisted of tree type, location on the tree, and the vitality of each. Tree species were lumped into pines and hardwoods. Locations were trunk below the tree crown, trunk within the crown, limb, and pine cone. Trees and locations were classed as living or dead.

Although observations were made of all family members, only data for the adult male and female of each group were analyzed because other birds were not present throughout the study. The 5-minute observation bout was used as the unit of analysis because observations made at 15-second intervals were not independent (Repasky 1984). Substrates were divided into mutually exclusive pairs for analysis, including pine and non-pine substrates, living and dead pines, trunk and non-trunk surfaces of live pines, trunk-within-crown and trunk-belowcrown of live pines, and dead limb and other components of non-trunk areas of live pines. The proportion of foraging time spent upon one category of each pair was calculated for each bout. Least squares means (SAS Institute 1982b) from analyses of variance were used to estimate substrate use because of differences between time periods and between sexes in substrate use and sample size. Calculations were by weighted least squares regression to satisfy the assumption of homogeneity of variance (Neter and Wasserman 1974).

Foraging behaviors were analyzed in a manner similar to that used for substrates. The proportion of foraging time spent in each behavior was calculated for each observation bout. Least squares means were estimated using weighted least squares ANOVAs.

The independence of foraging behavior and substrate was tested with a 2-way chi-square contingency table. A pool of presumably independent observations was created by randomly selecting one observation from each substrate in each 5-minute observation bout. All observations from the month and individual with the least number of observations were used in the test with equal numbers of randomly chosen observations for other months and individuals. In this analysis, substrates were pooled to hardwoods, dead pine surfaces, non-trunk surfaces of living pines, live pine trunk within the crown, and live pine trunk below the crown.

Overlap between the foraging niches of the adults of each group was calculated monthly as  $\alpha$  from Levins (1968). Calculations were based on the proportions of total foraging time spent on the substrates. These were calculated from the least squares means obtained from the analyses described above. For example, the proportion of foraging time spent on dead limbs of living pines was calculated as the proportion of foraging time spent on pines times the proportion of pine foraging time spent on living pines times the proportion of non-trunk foraging time spent on dead limbs. Categories used in the calculations were dead pines, live limbs on live pines, dead limbs on live pines, pine cones, trunk within crown of live pines, trunk below crown of live pines, and hardwoods.

Statistical summaries and tests were performed with the Statistical Analysis System (SAS Institute 1982a, 1982b). Analyses of variance were performed with the General Linear Models (GLM) procedure. Contingency table tests were performed with the frequency (FREQ) procedure.

#### **RESULTS AND DISCUSSION**

#### HOME RANGE USE

The year-round range of family group A was 180 ha and that for group B was 139 ha. Territories comprised 35% and 62% of the year-round home ranges, respectively. The two groups spent 26% and 16%, respectively, of foraging time outside of the territories.

Pine characteristics of foraging areas were compared with those of the overall home ranges. Significant differences were found for group A but not for group B (Tables 1 and 2). For group A, median pine bole surface density and median tree density were greater in areas used than within the home range at large. Median DBH was less. Results for family group B were opposite to those for group A, although the comparisons were not statistically significant. Median pine bole surface density and tree density in foraging areas were less in areas available than in foraging areas, whereas median DBH was nearly identical. When the same comparisons were made for individual tracking periods, the results were similar to the overall comparisons for each group (Tables I and 2), although few of the differences were significant.

Two forest stand characteristics that are expected to be positively related to foraging habitat quality are negatively related to one another in nature. Tree density is expected to be positively related to foraging quality because of improved insect habitat quality and decreasing flight distance with increasing tree density (Wood 1983). Habitat quality is also expected to increase as tree size increases because larger trees should provide better prey habitat (Travis 1977, Jackson 1979) and more foragable surface per distance travelled between trees (Hooper and Lennartz 1981). In natural stands, however, tree size and density are inversely related to one another (Wahlenberg 1946). DeLotelle et al. (1987) demonstrated that red-cockaded woodpeckers prefer stands of larger tree size when density is held constant and that they prefer stands of greater density when tree size is held constant. The type of stands selected for foraging by a family group is likely to depend on the variation in stand density relative to variation in tree size.

Variation in density was greater than variation in tree size in the home ranges studied. The coefficients of variation of tree density (group

		Foraging areas						
	Home range	1979			1980			
Measure		Sept.	Nov.	Jan.	Mar.	May	July	Pooled
Bole surface	1007.0	1053.0	886.0	1438.0**	1145.0	1199.0	1234.0	1200.0*
density (m <sup>2</sup> /ha)	(100)	(25)	(25)	(25)	(25)	(25)	(24)	(149)
Tree density	125.0	160.0	94.0	245.0***	166.0	205.0*	191.0	171.0*
(trees/ha)	(100)	(25)	(25)	(25)	(25)	(25)	(24)	(149)
DBH (cm)	30.3	28.2	33.5	23.4**	26.0	26.3*	28.8	26.8*
	(93)	(24)	(24)	(25)	(25)	(25)	(24)	(147)

Table 1. Median values and sample sizes (in parentheses) of pine characteristics of the overall home range and foraging areas used by family group  $A^{a,b}$ .

<sup>a</sup> Wilcoxon two-sample tests were used to compare pine characteristics of foraging areas with those of the overall home range.

b \* = P < 0.05; \*\* = P < 0.01; \*\*\* = P < 0.001.

Table 2. Median values and sample sizes (in parentheses) of pine characteristics of the overall home range and foraging areas used by family group  $B^{a,b}$ .

		Foraging areas						
	Home range	1979			1980			
Measure		Aug.	Oct.	Dec.	Feb.	Apr.	June	Pooled
Bole surface	1879.0	1385.0*	1648.0	1759.0	1641.0	1570.0	1773.0	1644.0
density (m <sup>2</sup> /ha)	(49)	(25)	(25)	(25)	(25)	(25)	(24)	(149)
Tree density	263.0	143.0**	202.0	212.0	223.0	190.0	301.0	212.0
(trees/ha)	(49)	(25)	(25)	(25)	(25)	(25)	(24)	(149)
DBH (cm)	28.3	31.6*	24.8	26.3	29.5	28.4	22.7	28.2
	(46)	(25)	(25)	(24)	(25)	(25)	(24)	(148)

<sup>a</sup>Wilcoxon two-sample tests were used to compare pine characteristics of foraging areas with those of the overall home range.

b \* = P < 0.05; \*\* = P < 0.01; \*\*\* = P < 0.001.

A: 124, B: 118) were much larger than the coefficients of variation of tree size (group A: 28, B: 38). Group A selected areas of greater tree density and smaller tree size, as might be expected.

Group B did not select foraging areas on the basis of any of the variables that we measured. Perhaps this was due to conditions within its home range. Tree density was nearly twice that in group A's home range, and the understory was much lower than it was in group A's home range. Group B, therefore, may have had less need to select foraging areas on the basis of habitat quality than did group A.

## FORAGING DATA

*Foraging substrates.* Most foraging took place on pines (Table 3). Living pines were used much more than dead pines. Males spent more time than females foraging on limbs, and when foraging on the trunk, males generally foraged higher than females.

With two exceptions, these results are qualitatively similar to those for red-cockaded woodpeckers in other regions (Ligon 1968, 1970, Morse 1972, Skorupa and McFarlane 1976, Nesbitt et al. 1978, Skorupa 1979, Ramey 1980, Hooper and Lennartz 1981, Porter et al. 1985). First, the dead trees that were used extensively during December were different from those used at other times of the year and in other regions. Dead trees used outside of December were recently dead and retained pine needles as described by Hooper and Lennartz (1981). By contrast, dead trees used in December had long been dead and were missing large limbs and some bark. None had died of lightning strikes during the previous summer. Extensive use of long-dead pines has not been reported previously, although Hooper and Lennartz (1981) reported a single observation. Second, the extraction of seeds from open longleaf pine cones has not been reported previously. Hooper and Lennartz (1981) reported use during September and October of green, unopened longleaf pine cones that contained insect larvae. During November and December, however, we observed seeds being removed from open cones, although this activity was a small percentage of foraging time and did not occur during sampling.

Foraging behavior. Most foraging time was spent peering and poking (group A: 55%, group B: 53%; Table 4). Less time was spent pecking (group A: 27%, group B: 36%; Table 4), and the least time was spent gleaning (group A: 15%, group B: 9%; Table 4).

Foraging substrate and behavior were not independent (group A:  $\chi^2 = 43.6$ , df = 8, P < 0.001; group B:  $\chi^2 = 38.6$ , df = 8, P < 0.001), indicating that some seasonal variation in foraging behavior was attributable to changes in substrate use. Too few data were available to estimate the proportion of time spent in various foraging behaviors on each substrate. Niche overlap was therefore based on substrate use.

Month	Sex	Pine vs. hardwood	Live pine vs. dead pine	Pine trunk vs. pine limbs	Trunk below crown vs. trunk within crown	Live limb vs. dead limb & pine cone <sup>b</sup>
				Group A		
9/79	Μ	$98 \pm 2$	$100 \pm 1$	$27 \pm 9$	$0 \pm 7$	$10 \pm 6$
	F	$91 \pm 2$	$98 \pm 2$	$90 \pm 3$	$51 \pm 6$	$35 \pm 19$
11/79	Μ	$95 \pm 5$	$95 \pm 4$	$56 \pm 16$	-1 ± 9	$5 \pm 18$
5	F	$90 \pm 2$	$91 \pm 5$	$99 \pm 3$	$86 \pm 9$	$50 \pm 105$
1/80	Μ	$100 \pm 1$	99 ± 1	$68 \pm 8$	$46 \pm 10$	$14 \pm 9$
	F	$100 \pm 1$	$100 \pm 1$	$98 \pm 3$	$66 \pm 11$	$0 \pm 15$
3/80	Μ	$100 \pm < 1$	$98 \pm 1$	$70 \pm 4$	$12 \pm 3$	$22 \pm 5$
	F	98 ± 1	$95 \pm 3$	$95 \pm 2$	$34 \pm 4$	$77 \pm 15$
5/80	Μ	$100 \pm 1$	$100 \pm 1$	$81 \pm 3$	$85 \pm 3$	$13 \pm 4$
	F	$100 \pm 1$	99 ± 1	$100 \pm 1$	$96 \pm 4$	
7/80	М	$97 \pm 2$	$100 \pm 1$	$28 \pm 8$	$9 \pm 10$	$24 \pm 10$
	F	97 ± 2	$96 \pm 2$	$98 \pm 2$	$72 \pm 5$	$4 \pm 14$
				Group B		
8/79	М	$100 \pm 1$	$100 \pm 1$	$80 \pm 9$	$10 \pm 7$	$34 \pm 14$
	F	98 ± 1	99 ± 1	$94 \pm 3$	$58 \pm 8$	$65 \pm 17$
10/79	М	$99 \pm 1$	99 ± 1	$56 \pm 8$	$6 \pm 5$	$28 \pm 8$
	F	$98 \pm 2$	$100 \pm 1$	61 ± 7	$20 \pm 9$	$18 \pm 7$
12/79	Μ	99 ± 1	$63 \pm 7$	$91 \pm 5$	$25 \pm 12$	$51 \pm 17$
	F	$100 \pm 1$	$84 \pm 6$	$100 \pm 1$	$61 \pm 8$	$0 \pm 1.6$
2/80	М	96 ± 2	$100 \pm 1$	$65 \pm 6$	$30 \pm 7$	$9\pm5$
	F	96 ± 1	$100 \pm 1$	$98 \pm 2$	$52 \pm 6$	$33 \pm 36$
4/80	М	$99 \pm < 1$	99 ± 2	$77 \pm 3$	$54 \pm 4$	$58 \pm 6$
4	F	97 ± 1	98 ± 2	$90 \pm 2$	$80 \pm 4$	$100 \pm 2$
6/80	М	$96 \pm 1$	$100 \pm 1$	$56 \pm 5$	$12 \pm 5$	$25\pm 6$
	F	$100 \pm 1$	$100 \pm 1$	$95 \pm 3$	$38 \pm 8$	$0 \pm 11$

Table 3. Percentage of foraging time spent on various types of substrates<sup>a</sup>.

<sup>a</sup> Percentages, expressed as the amount of time on the first-mentioned substrate versus some alternative substrate, and standard errors were calculated as least squares means in analyses of variance.

<sup>b</sup> Use of pine cones occurred only during the period from September through December. During September the male and female used cones for 8 and 10%, respectively, of time spent off of the trunk. The figures for October were 51 and 71%, respectively. Use of cones during November and December was too infrequent to be captured by the sampling scheme. Niche overlap. Maximum overlap between sexes occurred at different times for the two groups (Fig. 1). For group A, overlap was greatest in May, when nestlings were tended and the male foraged uncharacteristically low and upon the trunk. Overlap in group B was greatest in October, when pine cones were used by both sexes and the female foraged uncharacteristically high upon the trunk. Minimum overlap between the sexes occurred in the late fall and early winter and then again during summer (Fig. 1).

Sex-specific foraging is a means by which sexes can reduce competition for resources (Selander 1966, Ligon 1968). Overlap is expected to decrease as food becomes less abundant (Wallace 1974, Hogstad 1977), although Winkler (1979) noted that Strickland's woodpecker, Picoides stricklandi (Malherbe), exhibited the least amount of overlap when opportunistic conditions permitted sex-specific foraging. Lack (1954) suggested that winter and the post-fledging portion of summer may be times of food limitation for birds. Reduced overlap during summer does not seem to reflect opportunistic use of resources, for no such activity was recorded in the component variables. It may reflect resource partitioning with increased group size after fledging. This may seem an unlikely necessity because Hooper et al. (1982) concluded that some home ranges contain more resources than necessary. However, the problem of resource depletion within the proximity of a predator (Charnov et al. 1976) is magnified with increasing group size, and reduced foraging overlap may be a solution to that problem. It is also an alternative to changing home range size in times of relative food scarcity (Selander 1966).

Foraging time. Red-cockaded woodpeckers were active during most of the available daylight hours. The interval between leaving cavities in the morning and roosting averaged 93% of the time from sunrise to sunset, ranging monthly from 83% to 100% (Table 5). Only the means for January, February, and March were less than 90%. The percentage of active time spent foraging was least in May and June and greatest during December and January (Table 5). The number of hours of foraging per day, calculated as the product of the number of active hours and the proportion of time spent foraging, corresponded closely with the number of active hours per day (Table 5), being greatest in summer and least in winter.

Foraging activities should reflect the availability of food relative to needs. The proportion of daylight time spent in activity and foraging as a proportion of active time are expected to be greatest during the period of resource limitation. Hinde (1952) found that tits (*Parus* spp.) increased the proportion of daylight hours in which they were active during the winter. Gibb (1954) found that the proportion of time spent foraging

was greatest in December for four species of tits and greatest in February for a fifth species. Our finding that red-cockaded woodpeckers were least active during the winter is not evidence against the hypothesis that winter is the principal time of resource limitation for red-cockaded woodpeckers. It may reflect avoidance of unfavorable conditions by remaining in the cavity. In winter, the birds generally did not leave their cavities until the sun reached the trees, and then they often basked. Thus they may avoid pre-sunrise activity that is expensive for small birds (Morse 1970). The absolute number of hours spent foraging need not be greatest in the period of food limitation. In winter, activity is limited by daylight, and sufficient energy must be acquired to survive the night. As days lengthen, the potential for more activity increased (e.g. cavity construction, territorial defense, reproduction). Thus the energy budget increases and the absolute foraging time increases to meet these needs. Presumably this is offset, to some unknown degree, by differences in temperature and food abundance. Strain on the energy budget is probably best reflected by the percentage of the activity budget spent foraging. This was greatest during December and January.

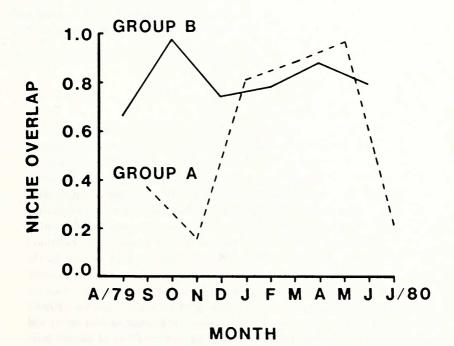


Fig. 1. Overlap in foraging substrate use between the sexes within 5-minute observation bouts.

		Fen	nale			N	fale	
Month	Peer & Poke	Peck	Glean	Other <sup>a</sup>	Peer & Poke	Peck	Glean	Other <sup>a</sup>
				Gro	up A			
9	$47 \pm 6$	$35\pm5$	$12 \pm 4$	6	$\frac{1}{24 \pm 10}$	$56 \pm 12$	$11 \pm 5$	9
11	$50\pm7$	$17 \pm 5$	$32\pm 6$	1	$70 \pm 16$	$18 \pm 12$	$13 \pm 15$	-1
1	$73 \pm 7$	$12 \pm 5$	$13 \pm 4$	2	$66 \pm 7$	$25 \pm 7$	$8 \pm 3$	1
3	$54 \pm 3$	$23 \pm 3$	$23 \pm 3$	0	$52 \pm 3$	$41 \pm 4$	7 ± 1	0
5	$63 \pm 7$	$23 \pm 5$	$11 \pm 5$	3	$56 \pm 4$	$28 \pm 3$	$15 \pm 3$	1
7	$59\pm5$	$27 \pm 5$	$14 \pm 3$	0	$48 \pm 8$	$39 \pm 9$	$16 \pm 5$	-3
				Gr	oup B			
8	$54\pm5$	$32 \pm 5$	$13 \pm 3$	1	$40 \pm 11$	$29 \pm 10$	$20 \pm 6$	11
10	41 ± 7	$53 \pm 7$	$4\pm1$	2	$39 \pm 6$	$54 \pm 7$	$7\pm2$	0
12	$57 \pm 4$	$32 \pm 4$	$6\pm 2$	5	$55\pm5$	$35\pm 6$	$10 \pm 2$	0
2	$56 \pm 4$	$37 \pm 3$	$7 \pm 1$	0	$47 \pm 5$	$44 \pm 6$	$8\pm3$	1
4	$74 \pm 2$	$21 \pm 2$	$5\pm1$	0	$60 \pm 2$	$28 \pm 2$	$12 \pm 1$	0
6	$65 \pm 6$	$29 \pm 6$	$5\pm 2$	1	$45 \pm 4$	$40 \pm 4$	$15 \pm 2$	0

Table 4. Mean and standard error of the percentage of foraging time spent using various foraging methods.

<sup>a</sup> "Other" time was calculated as the percentage complement of peering and poking, pecking, gleaning; so, it also includes estimation error associated with these behaviors.

#### SYNTHESIS

Several pieces of evidence intersect to suggest that if food is limiting to red-cockaded woodpeckers, it may be least available during early winter. Foraging occupied the greatest portion of the day in December and January, and overlap in substrate use between the sexes was low during November and December. Furthermore, supplanting attacks for foraging sites among family group members peaked during December and January, and supplanting attacks by red-bellied woodpeckers, Melanerpes carolinus (L.), peaked during January and February (Repasky 1984). Skorupa (1979) has also argued that winter is the period of resource limitation on the basis of seasonal territory dynamics. If foraging habitat quality were related to habitat structure, habitat preference would be expected to be strongest during the period of food limitation. The family group that exhibited preference in this study did so most strongly during January, and it preferred areas of higher pine density and surface area and smaller tree diameter within its home range.

	Acti	ve time	Foraging time		
Month	Hours	Percentage of day	Percentage of active time	Hours	
		Group A			
9	11.8	91	84	9.9	
11	9.2	92	70	6.4	
1	8.6	86	85	7.3	
3	10.6	88	72	7.6	
5	13.8	94	65	8.9	
7	14.0	100	71	9.9	
		Group B			
8	13.0	100	64	8.3	
10	10.2	93	75	7.7	
12	8.6	95	79	6.8	
2	9.2	83	70	6.4	
4	13.0	100	63	8.2	
6	13.6	91	59	8.0	

Table 5. Mean daily activity budgets.

Our data do not permit firm conclusions about food limitation and habitat preference, but they can be used to suggest areas of future research. We believe that it is worth investigating whether winter survival of red-cockaded woodpeckers is a significant factor influencing population size and structure and influenced by winter foraging conditions, and if so, whether foraging conditions are related to manageable characteristics of forests.

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